Oldest cingulate skulls provide congruence between morphological and molecular scenarios of armadillo evolution

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The cingulates of the mammalian order Xenarthra present a typical case of disagreement between molecular and morphological phylogenetic studies. We report here the discovery of two new skulls from the Late Oligocene Salla Beds of Bolivia (approx. 26 Ma), which are the oldest known well-preserved cranial remains of the group. A new taxon is described: *Kuntinaru boliviensis* gen. et sp. nov. A phylogenetic analysis clusters *K. boliviensis* together with the armadillo subfamily Tolypeutinae. These skulls document an early spotty occurrence for the Tolypeutinae at 26 Ma, in agreement with the temporal predictions of previous molecular studies. The fossil record of tolypeutines is now characterized by a unique occurrence in the Late Oligocene, and a subsequent 12 Myr lack in the fossil record. It is noteworthy that the tolypeutines remain decidedly marginal in the Late Palaeogene and Early Neogene deposits, whereas other cingulate groups diversify. Also, the anatomical phylogenetic analysis herein, which includes *K. boliviensis*, is congruent with recent molecular phylogenetic analyses. *Kuntinaru boliviensis* is the oldest confident calibration point available for the whole Cingulata.

Keywords: Palaeogene; Tolypeutinae; Bolivia; phylogeny; fossil record; calibration point

1. INTRODUCTION

The extant Xenarthra constitute one of the four recently recognized major clades of extant placental mammals [1,2], but also the only living testimony of the great endemic evolution undergone by placental mammals in South America. The Xenarthra gather the extant sloths, anteaters and armadillos, and a large number of much diversified fossil taxa. As such, the group offers a unique opportunity to use evidence from both molecular and morpho-palaeontological data to reveal a part of this very peculiar history.

Until now, however, these two approaches have worked largely apart from each other and resulted in some conflicts regarding the phylogeny of xenarthrans. A typical case is evident in the phylogeny of the diverse Cingulata (e.g. [3,4]), which contains not only the modest current representatives of armadillos, but also a great diversity of fossil armadillos and the herbivorous pampatheres and glyptodonts [5,6]. As well as pure phylogenetic disagreements, the dispute concerns temporal predictions made by molecular studies on the time divergences of various clades and their effective recognition in the fossil record, which generally occurs much later. The scarcity of the Palaeogene fossil record of cingulates is certainly a major reason for this

incongruence. It consists only of very rare cranial bones, a few isolated scutes and postcranial elements (e.g. [7–9]). The first well-preserved skulls and skeletons allowing extensive anatomical descriptions are only known from the Early Miocene Santacrucian South American Land Mammal Ages (SALMA), around 16–17 Ma [10,11].

The Late Oligocene Deseadan Salla Beds of Bolivia have yielded one of the richest South American Palaeogene mammal faunas, dated around 25–26 Ma [12]. We provide here the description of two new well-preserved cingulate skulls from this locality. The two specimens constitute, together with an undescribed peltephilid skull from the same locality [13], the oldest well-preserved cranial remains from Cingulata (and Xenarthra as a whole).

These skulls document an early spotty occurrence for the Tolypeutinae at 26 Ma, in agreement with the temporal estimates made by previous molecular studies [14]. The fossil record of tolypeutines is, however, still characterized by a great rarity of remains in the Late Palaeogene and Early Neogene, with this new unique occurrence in the Late Oligocene and a subsequent 12 Myr lack in the fossil record. Moreover, the cladistic analysis we performed including this new taxon provides interesting congruence with molecular studies on the phylogenetic relationships within the Cingulata. This discovery also allows the establishment of the oldest confident calibration point available in the whole Cingulata.
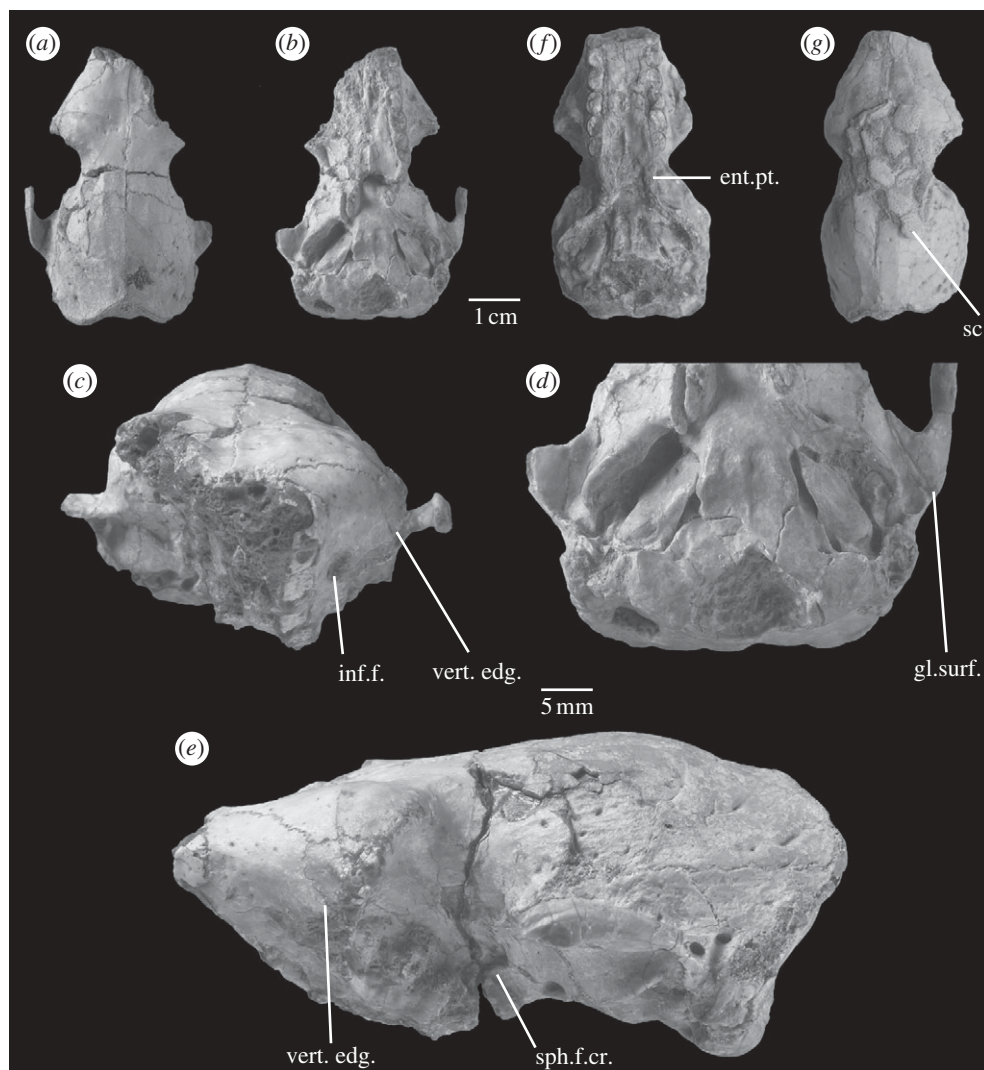
Figure 1. *Kuntinaru boliviensis* gen and sp. nov. Detailed views of the cranial anatomy. (*a*–*e*) MNHN-SAL 1024, respectively, (*a*) dorsal, (*b*) ventral, (*c*) rostral, (*d*) zoom on auditory region and (*e*) left lateral views. (*f*) Ventral and (*g*) dorsal views of MNHN-SAL 3. *Abbreviations*: gl.surf., elongated glenoid surface; inf.f., infraorbital foramen; ent.pt., entopterygoid crests in line with the tooth rows; sc., dermal scutes of the cephalic shield; sph.f.cr., crest anteroventral to the sphenorbital fissure; vert.edg., vertical anterior edge of orbit.

2. RESULTS

(a) *Description and comparison*

Xenarthra Cope, 1889.

    Cingulata Illiger, 1811.

        Dasypodidae Gray, 1821.

           Tolypeutinae Gray, 1865.

              Kuntinaru gen. nov.

                  Kuntinaru boliviensis sp. nov.

Synonymy: Dasypodidae cf. *Prozaedyus* and/or *Proeutatus* sp. [15].

Holotype: MNHN-SAL 1024, skull missing the apex of the rostrum, but preserving most of the left tooth row, and all of the posterior half of cranium, except the zygomatic arches (figure 1*a*–*e*), collected by one of us (C.M.).

Paratype: MNHN-SAL 3, skull missing the apex of the rostrum but preserving the six posterior teeth on both sides, the orbitotemporal fossae and the anterior half of the auditory region (figure 1*f,g*), collected by R. Hoffstetter.

Locality: Salla, Department of La Paz, Bolivia.

Distribution: Deseadan SALMA, Late Oligocene.

Etymology: *Kuntinaru*, 'ghost' in Aymara, the native spoken language in Salla, refers to the ghost-like isolated occurrence of this taxon and the subsequent 12 Myr absence of the tolypeutines in the fossil record. *Boliviensis* is for the occurrence of this taxon in Bolivia.

Diagnosis (both genus and species, for monotypy): *Kuntinaru* is a member of the Tolypeutinae because it exhibits the following tolypeutine apomorphies: a vertical anterior edge of the orbit and a surface anterior to the postglenoid foramen elongated antero-posteriorly, not delimited posteriorly by a line continuous with the lateral edge of the zygomatic arch; *Kuntinaru* differs from all armadillos by the presence of a thick crest anterolateral to the middle-ear cavity; differs from extant tolypeutines in possessing the following plesiomorph features: an infra-orbital foramen approximated to the anterior root of the zygomatic arch and a well-marked orbital muscular crest; differs from *Cabassous* and *Priodontes* in possessing the following plesiomorph features: a distinct antorbital depression and crest for nasolabialis muscle insertion, and a stylomastoid foramen medial to the paroccipital process of petrosal and not posteromedial; differs from the early-diverging euphractine *Prozaedyus* by the toly-peutines apomorphies cited above and in possessing the

following plesiomorph features: straight entopterygoid crests in line with the tooth rows, and posterior part of the palate flat; differs from earlier-diverging cingulates like *Peltephilus* and *Stegotherium* in exhibiting notably the following apomorphies uniting tolypeutines, euphractines and glyptodontoids (in addition to the tolypeutine apomorphies already mentioned above): a sinuous zygomatic arch profile in lateral view and a notch/depression in the medial internal wall of the occipital condyles; and differs further from *Peltephilus* in having a highly situated glenoid fossa.

The following description provides only some important characters in *Kuntinaru* (more is provided in the electronic supplementary material, S1 and S2).

On the rostrum, the infraorbital foramen is bordered posterodorsally by a faint crest sloping backwards. This crest runs from the medial edge of the anterior zygomatic root and is directed towards the nasals' posterior extremities. It is present and well-developed in most armadillos, but generally weak in *Tolypeutes*, as in *Kuntinaru*, and absent in *Cabassous* and *Priodontes*. Below this crest, the development of the antorbital depression (or fossa) is reduced in these latter taxa, as well as, to some extent, in *Kuntinaru*. The location of the infraorbital foramen relative to the anterior root of the zygomatic arch is also noteworthy. In *Kuntinaru*, and in most armadillos, it opens close to the anterior root of the zygomatic arch, whereas it is more anterior in *Tolypeutes*, *Cabassous* and *Priodontes*.

The facial area anterior to the orbit, especially the lacrimal, is oriented vertically in *Kuntinaru* and is perpendicular to the frontal roof (figure 1*c*). This is also true in *Tolypeutes*, *Cabassous* and *Priodontes*, but not in the other armadillos, where the facial surface of the lacrimal is oblique. From an anterior perspective, this feature is associated with a vertical orientation of the anterior edge of the orbit in both extant Tolypeutinae and *Kuntinaru*. The anterior edge of the orbit is not fully preserved in *Kuntinaru* skulls but it clearly appears that the anterior edge of the orbit had a vertical orientation considering the vertical orientation of the lacrimal and the strictly ventral connection (not ventrolateral) of the anterior zygomatic root with the face.

The entopterygoid crests are straight and aligned with the tooth rows in *Kuntinaru* (figure 1*f*). In fact, in armadillos there are different shapes in the direction of the posterolateral line of the palate from the most posterior tooth up to the anterolateral border of the entopterygoid crests. This line is straight, more or less anteroposterior and aligned with the tooth rows in *Tolypeutes*, *Cabassous* (except *Cabassous centralis*), *Priodontes*, *Dasypus*, *Stegotherium* and *Eutatus*, but also in extant sloths, whereas it is much more concave and oblique, directed medially backwards, in the extant euphractines and *Prozaedyus*.

The palate is flat posteriorly in *Kuntinaru*, a condition found in the extant Tolypeutinae and Dasypodinae, which contrasts with the concavity observed in the extant euphractines, *Prozaedyus*, *Proeutatus* and the glyptodont *Propalaeohoplophorus*.

In the orbitotemporal fossa, *Kuntinaru* exhibits a ridge continuous with the posterior edge of the sphenorbital fissure anteroventrally, like extant tolypeutines. This ridge defines the lateral wall of a deep gutter running forward up to the sphenopalatine foramen (figure 1*e*). This

region is damaged (i.e. distorted) in *Kuntinaru*, but remnants of such a crest are clearly present.

While flattened, we observed that the glenoid surface in *Kuntinaru* is barely longer than it is wide, but clearly less elongated than in *Cabassous*, *Tolypeutes* and *Priodontes* (figure 1*d*). It is also different from *Euphractus*, *Chaetophractus*, *Dasypus* and *Zaedyus*, in which glenoid width is greater than its length. Anterior to the post-glenoid foramen, the glenoid surface of *Euphractus*, *Chaetophractus*, *Dasypus* and *Zaedyus* is delimited backwards by a low crest continuous with the lateral edge of the zygomatic arch. Such a crest is absent in *Kuntinaru* and extant tolypeutines.

The auditory region of *Kuntinaru* is very well preserved and delivers a wealth of anatomical information that is detailed and illustrated in the electronic supplementary material, S1 and S2. Among the observations made therein, it can be pointed out here that *Kuntinaru* presents an overall auditory region especially reminiscent of *Tolypeutes*: a likely absence of a well-ossified bulla, like, notably, in tolypeutines and dasypodines; an elongated epitympanic wing on the petrosal, greatly resembling *Tolypeutes*, *Cabassous* and the glyptodontoids; a well-marked crest bordering laterally the postglenoid foramen as in *Tolypeutes*; and a wide and shallow epitympanic recess as in *Tolypeutes* and *Priodontes*. However, the two latter characters could unfortunately not be checked in many armadillos and should therefore be considered here as suggestive rather than definite support for exclusive resemblance of the auditory region of *Kuntinaru* with that of some tolypeutines.

(b) Phylogenetic analysis

A cladistic analysis comprising 22 taxa and 125 characters has been performed in order to explore the phylogenetic relationships of *Kuntinaru* and armadillos; 112 characters come from Gaudin & Wible [4], 17 of which have been slightly modified; 13 characters are new. The taxonomic sample is the same as Gaudin & Wible [4], with the addition of *Kuntinaru*. The character list and data matrix can be consulted in the electronic supplementary material, S1. The analysis has been performed with TNT [16], with the traditional search option, 100 replications and the tree bisection reconnection swapping algorithm.

The analysis resulted in four most parsimonious cladograms of 455 steps. The indices of the present cladograms are very similar to those of Gaudin & Wible [4]: consistency index = 0.42 and retention index = 0.54. The strict consensus (462 steps, consistency index = 0.41, retention index = 0.53) is presented in figure 2.

The Cingulata (clade A) are monophyletic. The earliest-diverging cingulate is *Peltephilus*. Within the immediate less inclusive cingulate clade B, the dasypodines (clade C; *sensu* [21]) are monophyletic. They constitute the sister taxa of clade D, gathering the tolypeutines, euphractines (term used throughout to gather Euphractini and Eutatini [21]) and the glyptodontoids (a term used throughout to gather pampatheres and glyptodonts [21]). Clade E clusters *Kuntinaru*, as the earliest-diverging member, together with the monophyletic extant tolypeutines (clade F), among which *Cabassous* and *Priodontes* (clade G) are closer to each other than to *Tolypeutes*. Within clade D, clade including *Kuntinaru* and extant tolypeutines (clade E) is the sister
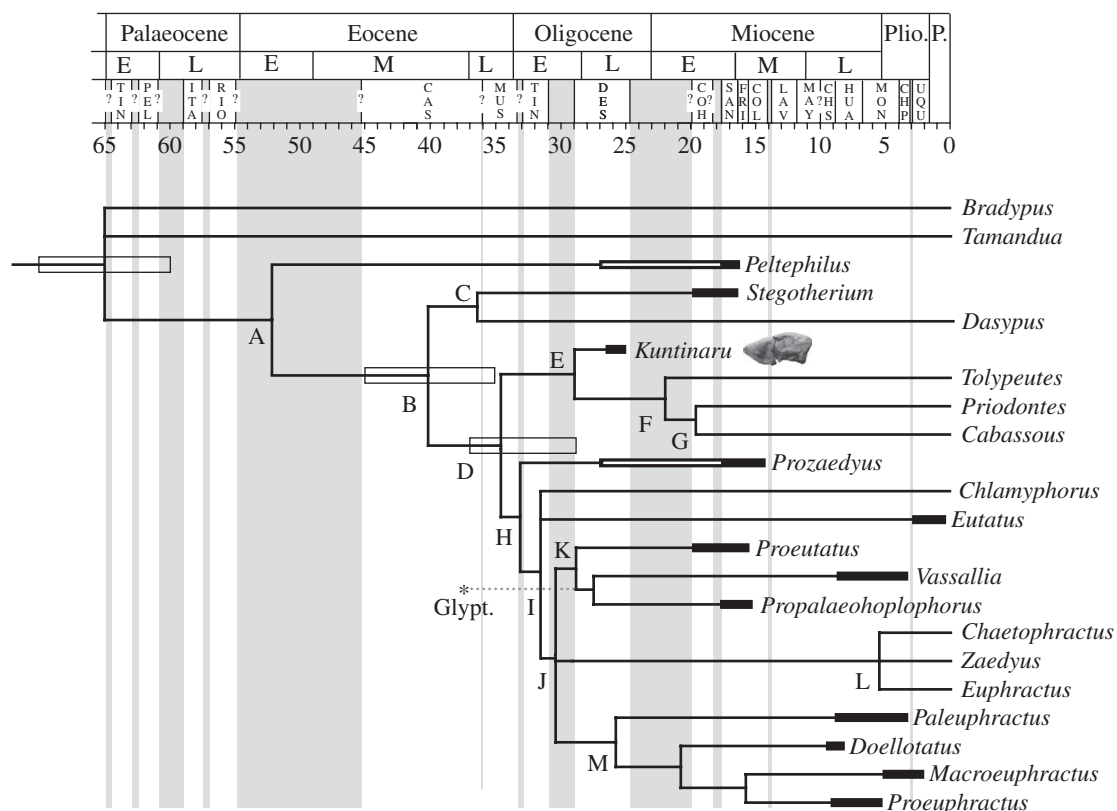
Figure 2. Phylogeny, fossil record and molecular inferences for Cingulata. Phylogenetic tree of cingulates constructed based upon the strict consensus cladogram issued from the cladistic analysis of 22 cingulate taxa. The lower part of the time-scale represents the South American Land Mammal Ages (SALMA) and the grey shaded areas correspond to the hiatus in the fossil record (ages in Myr; after [17−20]). Upper case letters refer to the principal nodes. The confidence limits on divergence time estimates for some crown clades [14] are represented by empty rectangles at nodes. The time range of fossil genera is represented in rectangles: a white rectangle denotes a genus only known by isolated elements (e.g. scutes) at this time; a black rectangle denotes a genus known by nearly complete skulls. The occurrence of Casamayoran scutes referable to the Glyptodontoidea (here including any taxon closer to *Vassalia* or *Propalaeohoplophorus* than to *Proeutatus*) is denoted by an asterisk. The temporal range of taxa comes from [21,22].

taxon of the larger clade H, clustering the euphractines and the glyptodontoids. *Prozaedyus* is the earliest-diverging member of the latter clade. The immediate less inclusive cingulate clade I exhibits a basal tritomy with *Eutatus*, *Chlamyphorus* and clade J, gathering the remaining euphractines and the glyptodontoids. This clade J presents a basal tritomy with clade K, uniting *Proeutatus* with the glyptodontoids, clade L allying the extant *Chaetophractus*, *Zaedyus* and *Euphractus*, and clade M clustering the fossil euphractine genera *Paleuphractus*, *Macroeuphractus*, *Doellotatus* and *Proeuphractus*.

3. DISCUSSION AND IMPLICATIONS

(a) *The phylogeny of the Cingulata*

The phylogenetic analysis supports the monophyly of the extant Tolypeutinae and *Kuntinaru* as an early-diverging tolypeutine. Given the pattern of relationships obtained for the Tolypeutinae, we could consider the clade clustering the three extant genera as crown tolypeutine and *Kuntinaru* as a stem tolypeutine. However, we rather favour a total-group concept [23], the common practice in Cingulata, and therefore classify *Kuntinaru* as a member of the Tolypeutinae. The monophyly of the Tolypeutinae is also clearly supported by molecular studies [3,14,24,25], and by recent analyses including postcranial morphology [26,27]. The previous analysis

of Gaudin & Wible [4] based on craniodental morphology argued the Tolypeutinae may form a paraphyletic assemblage at the base of the Euphractinae–Glyptodontoidea clade. New characters provide here unambiguous support for the monophyly of the tolypeutines. Particularly, the results of the analysis highlight a progressive modification of the facial region just anterior to the orbit in the Tolypeutinae (see data matrix, character list, character distribution and Bremer support values in the electronic supplementary material, S1).

The analysis supports *Cabassous* as being more closely related to *Priodontes* than to *Tolypeutes*, which is in contradiction to the molecular hypotheses that instead cluster *Cabassous* with *Tolypeutes* [3,14,24,25]. Nevertheless, the clade *Cabassous–Priodontes* is strongly supported not only by characters of the whole cranial anatomy (Bremer support value > 5), but also by a dataset comprised of a large number of postcranial characters [26]. Möller-Krull *et al.* argued that 'it is possible that morphologically based cladistic reconstructions might have been confounded by the highly derived morphology of *Tolypeutes*' (p. 2580 in [3]). However, the present cladistic analysis clearly shows that *Cabassous* and *Priodontes* share a high number of derived morphological characters not present in *Tolypeutes*, which displays rather plesiomorphic features.

Actually, considering only the extant genera on the strict consensus cladogram obtained here, the pattern is very close to the one hypothesized by a recent series of molecular phylogenetic studies [3,14,24,25,28]. In both patterns, *Dasypus* is the earliest-diverging extant genus, the extant tolypeutines and extant euphractines form a distinct clade (clade D), the extant tolypeutines are monophyletic (clade F), and *Euphractus*, *Chaetophractus* and *Zaedyus* are united in a clade (clade J) that does not include *Chlamyphorus*. A recent molecular analysis [3] supported *Chlamyphorus* as being closer to the tolypeutines than to the extant euphractines. If our morphological analysis indeed locates *Chlamyphorus* farther than usual from the extant euphractines [4,29], it nevertheless still supports closer relationships of this genus with extant euphractines than with tolypeutines. This relationship is especially evidenced by the shared derived configuration of the posterior part of the palate in *Chlamyphorus*, *Zaedyus*, *Euphractus* and *Chaetophractus* (and fossil relatives). Obviously, more molecular and morphological investigations are needed to resolve this contradiction. Our analysis also supports a clade allying the Euphractinae and Glyptodontoidea, as in two recent morphological analyses [4,29]. As in these works, the Santacrucian *Prozaedyus* constitutes the earliest-diverging member of this clade, and the Eutatini constitute a polyphyletic assemblage with *Proeutatus* as the sister taxon of the Glyptodontoidea. The main difference with the Gaudin & Wible [4] study concerns the earlier divergence of *Chlamyphorus* in our analysis.

It is worth mentioning that it is the first time that a cladistic analysis based on morphology mirrors so much the results of molecular studies [3,14,24,25,28], a fact that gives credence to the phylogenetic conclusions.

(b) The fossil record and the dating of evolutionary events in Cingulata

In agreement with molecular studies [14], the present result implies that the Tolypeutinae as a whole may have differentiated at least 26 Myr ago and diverged before this date from the euphractines and the fossil glyptodontoids. *Kuntinaru* from Salla constitutes the unique referral to Tolypeutinae from this period. Conversely, referrals to the Euphractinae and the Glyptodontoidea are known in various Oligocene localities [7,30,31], and are even registered in the Late Eocene Mustersan and Casamayoran SALMA [7,9,32,33]. Moreover, the Glyptodontoidea may be present as early as the Late Palaeocene, as tarsal remains from the Brazilian locality of Itaborai have been referred (although with doubts) to the group [34]. In any case, referrals to the Glyptodontoidea and Euphractinae trace their presence back to at least the Casamayoran, 36 Ma [17]. From this, a major problem occurs relative to the emergence of the Glyptodontoidea. In the present analysis, and in others [4,27], the glyptodontoids are located as an apical group nested within the euphractines. Their occurrence in the fossil record at least 36 Myr ago thus argues for a much older origin for the Euphractinae–Glyptodontoidea clade, and for the entire cingulate radiation. This latter point is not confirmed by the Palaeocene and Eocene fossil record of cingulates, which, to date, is very defective. Actually, a divergence between the Euphractinae–Glyptodontoidea

and the Tolypeutinae at a time much earlier than 36 Ma is also in disagreement with the molecular estimates for the divergence of Euphractinae/Tolypeutinae ranging between 37 and 29 Ma [14]. A solution may be that the Glyptodontoidea occupy a more basal position on the cingulate phylogenetic tree. On this point, the Bremer support values may be indicative. The position of the Glyptodontoidea as an apical group among the Euphractinae is not very strongly supported. All nodes within clade H have a Bremer support value of 1 or 2. However, their presence in a common clade H with the Euphractinae is strongly supported (Bremer support value = 5). More investigations and new fossil discoveries will drive our understanding of the evolution of the Glyptodontoidea, and we hope this will resolve the incongruence between the phylogenies, fossil record and dating estimates. As such, ancient DNA studies could constitute a powerful approach to better reconstruct the phylogenetic position of this remarkable group, as has been already done with extinct ground sloths [35,36].

The recent molecular studies dated the emergence of the Tolypeutinae around the Early Oligocene, at the latest before 29 Ma [14]. However, until the present study, no tolypeutine fossil was known before the Middle Miocene (12–14 Ma; [37]). This, therefore, implied a huge ghost lineage of at least 15 Myr. Further, immediately younger remains recognized as Tolypeutinae were described from Early Pliocene deposits (i.e. not before 5.3 Ma [21]). By supporting the Late Oligocene *Kuntinaru* as an early-diverging tolypeutine, the present analysis argues that the tolypeutines are known by a unique occurrence in the Late Oligocene, and are thereafter characterized by a subsequent 12 Myr lack in the fossil record. The fact that tolypeutines remain marginal in the Late Palaeogene and Early Neogene deposits, whereas other groups diversify, recalls in some way the pattern called 'dead clade walking' [38], a term usually specifically applied to those taxa presenting survival without recovery after mass extinction. This absence could, however, simply result from a poor knowledge of the characteristic features that allow tolypeutines to be distinguished from other fossil cingulates (e.g. unrecognized scutes). Meanwhile, in the Miocene, the euphractines and glyptodontoids are relatively abundant in the fossil record. This hiatus in the tolypeutine fossil record may also be due to some peculiar ecological factors incompatible with the preservation of their skeletal remains.

The discovery of these new Oligocene cingulate skulls points out how patchy is our knowledge of early cingulate evolution, as is the case for all xenarthrans, and, above all, how spotty is their fossil record. In this context, the description of *Kuntinaru* remains is of crucial importance. Indeed, *Kuntinaru* constitutes the only Palaeogene armadillo taxon with such completeness—it preserves the most complete cranial skeleton of any Palaeogene cingulate—that was placed in a phylogenetic context. Its recognition as an early-diverging tolypeutine now confers to it the role of the oldest and best existing calibration point for molecular analyses among cingulates.

REFERENCES

1 Murphy, W. J. & Eizirik, E. 2009 Placental mammals (Eutheria). In *The timetree of life* (eds S. B. Hedges & S. Kumar), pp. 471–474. Oxford, UK: Oxford University Press.

2 Wible, J. R., Rougier, G. W., Novacek, M. J. & Asher, R. J. 2007 Cretaceous eutherians and Laurasian origin for placental mammals near the K/T boundary. *Nature* **447**, 1003–1006. (doi:10.1038/nature05854)

3 Möller-Krull, M., Delsuc, F., Churakov, G., Marker, C., Superina, M., Brosius, J., Douzery, E. J. P. & Schmitz, J. 2007 Retroposed elements and their flanking regions resolve the evolutionary history of xenarthran mammals (armadillos, anteaters, and sloths). *Mol. Biol. Evol.* **24**, 2573–2582. (doi:10.1093/molbev/msm201)

4 Gaudin, T. J. & Wible, J. R. 2006 The phylogeny of the living and extinct armadillos (Mammalia, Xenarthra, Cingulata): a craniodental analysis. In *Amniote paleobiology: perspectives on the evolution of mammals, birds, and reptiles* (eds M. T. Carrano, T. J. Gaudin, R. W. Blob & J. R. Wible), pp. 153–198. Chicago, IL: University of Chicago Press.

5 Gaudin, T. J. & McDonald, H. G. 2008 Morphology-based investigations of the phylogenetic relationships among extant and fossil xenarthrans. In *The biology of the Xenarthra* (eds S. F. Vizcaíno & W. J. Loughry), pp. 24–36. Florida, IL: University Press of Florida.

6 Fernicola, J. C., Vizcaíno, S. F. & Fariña, R. A. 2008 The evolution of armored xenarthrans and a phylogeny of the glyptodonts. In *The biology of the Xenarthra* (eds S. F. Vizcaíno & W. J. Loughry), pp. 79–85. Florida, IL: University Press of Florida.

7 Carlini, A. A., Ciancio, M. R., Flynn, J. J., Scillato-Yané, G. J. & Wyss, A. R. 2009 The phylogenetic and biostratigraphic significance of new armadillos (Mammalia, Xenarthra, Dasypodidae, Euphractinae) from the Tinguirirican (early Oligocene) of Chile. *J. Syst. Palaeontol.* **7**, 489–503. (doi:10.1017/S1477201908002708)

8 Bergqvist, L. P., Abrantes, E. A. L. & Avilla, L. d. S. 2004 The Xenarthra (Mammalia) of São José de Itaboraí Basin (upper Paleocene, Itaboraian), Rio de Janeiro, Brazil. *Geodiversitas* **26**, 323–337.

9 Simpson, G. G. 1948 The beginning of the age of mammals in South America. I. *Bull. Am. Mus. Nat. Hist.* **91**, 1–232.

10 Patterson, B., Segall, W. & Turnbull, W. B. 1989 The ear region in xenarthrans (= Edentata, Mammalia). Part I. Cingulates. *Fieldiana Geol. New Ser.* **18**, 1–46.

11 Scott, W. B. 1903–1904 Mammalia of the Santa Cruz Beds. Part I: Edentata. *Rep. Princet. Expeditions Patagonia* **5**, 1–364.

12 Kay, R. F., MacFadden, B. J., Madden, R. H., Sandeman, H. & Anaya, F. 1998 Revised age of the Salla beds, Bolivia, and its bearing on the age of the Deseadan South American Land Mammal 'Age'. *J. Vert. Paleontol.* **18**, 189–199. (doi:10.1080/02724634.1998.10011043)

13 Kearney, K. & Shockey, B. 2008 Oldest cranium of a horned armadillo (Peltephilidae, late Oligocene, Bolivia): clues regarding basal cingulate morphology. *J. Vert. Paleontol.* **28**, 99A.

14 Delsuc, F., Vizcaíno, S. F. & Douzery, E. J. P. 2004 Influence of tertiary paleoenvironmental changes on the diversification of South American mammals: a relaxed molecular clock study within xenarthrans. *BMC Evol. Biol.* **4**, 11. (doi:10.1186/1471-2148-4-11)

15 Hoffstetter, R. 1968 Un gisement de mammifères déséadiens (Oligocène inférieur) en Bolivie. *C. R. l'Acad. Sci.* **267**, 1095–1097.

16 Goloboff, P., Farris, J. & Nixon, K. 2003 TNT: tree analysis using new technology. Program and documentation. See http://www.zmuc.dk/public/phylogeny/tnt.

17 Kay, R. F., Madden, R. H., Vucetich, G. M., Carlini, A. A., Mazzoni, M. M., Re, G. H., Heizler, M. & Sandeman, H. 1999 Revised geochronology of the Casamayoran South American Land Mammal Age: climatic and biotic implications. *Proc. Natl Acad. Sci. USA* **96**, 13 235–13 240. (doi:10.1073/pnas.96.23.13235)

18 Flynn, J. J. & Swisher, C. C. 1995 Cenozoic South American Land Mammal Ages: correlation to global geochronologies. In *Geochronology, time scales, and global stratigraphic correlation* (eds W. A. Berggren, D. V. Kent, M. P. Aubry & J. Hardenbol), pp. 317–333. Tulsa, OK: Society of Sedimentary Geology. Special publication no. 54.

19 Flynn, J. J., Wyss, A. R., Croft, D. A. & Charrier, R. 2003 The Tinguiririca Fauna, Chile: biochronology, paleoecology, biogeography, and a new earliest Oligocene South American Land Mammal 'Age'. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **195**, 229–259. (doi:10.1016/S0031-0182(03)00360-2)

20 Croft, D. A. 2007 The middle Miocene (Laventan) Quebrada Honda Fauna, southern Bolivia, and a description of its notoungulates. *Palaeontology* **50**, 277–303. (doi:10.1111/j.1475-4983.2006.00610.x)

21 McKenna, M. C. & Bell, S. 1997 *Classification of mammals above the species level.* New York, NY: Columbia University Press.

22 Carlini, A. A., Ciancio, M. R. & Scillato-Yané, G. J. 2010 Middle Eocene—Early Miocene Dasypodidae (Xenarthra) of southern South America: faunal succession at Gran Barranca—biostratigraphy and paleoecology. In *The Paleontology of Gran Barranca: evolution and environmental change through the middle Cenozoic of Patagonia* (eds R. H. Madden, A. A. Carlini, M. G. Vucetich & R. F. Kay), pp. 106–129. Cambridge, UK: Cambridge University Press.

23 Donoghue, P. C. J. 2005 Saving the stem group—a contradiction in terms? *Paleobiology* **31**, 553–558. (doi:10.1098/rspb.2001.1702)

24 Delsuc, F., Scally, M., Madsen, O., Stanhope, M. J., de Jong, W. W., Catzeflis, F. M., Springer, M. S. & Douzery, E. J. P. 2002 Molecular phylogeny of living xenarthrans and the impact of character and taxon sampling on the placental tree rooting. *Mol. Biol. Evol.* **19**, 1656–1671.

25 Delsuc, F., Stanhope, M. J. & Douzery, E. J. P. 2003 Molecular systematics of armadillos (Xenarthra, Dasypodidae): contribution of maximum likelihood and Bayesian analyses of mitochondrial and nuclear genes. *Mol. Phylogenet. Evol.* **28**, 261–275. (doi:10.1016/S1055-7903(03)00111-8)

26 Abrantes, E. A. L. & Bergqvist, L. P. 2006 Proposta filogenética para os Dasypodidae (Mammalia: Cingulata). In *Paleontologia de Vertebrados: Grandes Temas e Contribuições Científicas* (eds V. Gallo, P. M. Brito, H. M. A. Silva & F. J. Figueirido), pp. 261–274. Rio de Janeiro, Brazil: Interciência Ltda.

27 Gaudin, T. & Bramblett, J. 2010 Phylogenetic analysis of extinct and extant Cingulata (Xenarthra, Mammalia) based on combined cranial and postcranial data. *J. Vert. Paleontol.* **30**, 95A.

28 Delsuc, F., Catzelfis, F. M., Stanhope, M. J. & Douzery, E. J. P. 2001 Saving the stem group—a contradiction in terms? *Proc. R. Soc. Lond. B* **268**, 1605–1615. (doi:10.1098/rspb.2001.1702)

29 Engelmann, G. F. 1985 The phylogeny of the Xenarthra. In *The evolution and ecology of armadillos, sloths and vermilinguas* (ed. G. G. Montgomery), pp. 51–63. Washington, DC: Smithsonian Institution Press.

30 Pujos, F. & de Iuliis, G. 2007 Late Oligocene Megatherioidea fauna (Mammalia: Xenarthra) from Salla-Luribay (Bolivia): new data on basal sloth radiation and Cingulata-Tardigrada split. *J. Vert. Paleontol.* **27**, 132–144. (doi:10.1671/0272-4634(2007)27[132:LOMFMX]2.0.CO;2)

31 Ameghino, F. 1897 Les mammifères crétacés de l'Argentine. Deuxième contribution à la connaissance de la faune mammalogique des couches à Pyrotherium. *Boletin del Instituto Geográfico Argentino* **18**, 406–521.

32 Pascual, R. & Ortiz-Jaureguizar, E. 2007 The Gondwanan and South American episodes: two major and unrelated moments in the history of the South American mammals. *J. Mamm. Evol.* **14**, 75–137. (doi:10.1007/s10914-007-9039-5)

33 Pascual, R., Vucetich, M. G., Scillato-Yané, G. J. & Bond, M. 1985 Main pathways of mammalian diversification in South America. In *The great American biotic interchange* (eds S. G. Stehli & S. D. Webb), pp. 219–247. New York, NY: Pleunum Press.

34 Cifelli, R. L. 1983 Eutherian tarsals from the late Paleocene of Brazil. *Am. Mus. Novitates* **2761**, 1–31.

35 Höss, M. & Pääbo, S. 1993 DNA extraction from Pleistocene bones by a silica-based purification method. *Nucleic Acids Res.* **21**, 3913–3915. (doi:10.1093/nar/21.16.3913)

36 Poinar, H., Kuch, M., McDonald, G., Martin, P. & Pääbo, S. 2003 Nuclear gene sequences from a late Pleistocene sloth coprolite. *Curr. Biol.* **13**, 1150–1152. (doi:10.1016/S0960-9822(03)00450-0)

37 Carlini, A. A., Vizcaíno, S. F. & Scillato-Yané, G. J. 1997 Armored Xenarthrans: a unique taxonomic and ecologic assemblage. In *Vertebrate palaeontology in the Neotropics. The Miocene fauna of La Venta, Colombia* (eds R. F. Kay, R. H. Madden, R. L. Cifelli & J. J. Flynn), pp. 213–226. Washington, DC: Smithsonian Institution Press.

38 Jablonski, D. 2002 Survival without recovery after mass extinctions. *Proc. Natl Acad. Sci. USA* **99**, 8139–8144. (doi:10.1073/pnas.102163299)